

Five New Morphotypes of *Phyllobothrium delphini* (Cestoda: Tetraphyllidea). Their Relationship to Existing Morphotypes, and Their Zoogeography

Jacqueline Testa and Murray D. Dailey

Abstract.—*Phyllobothrium delphini* (Bosc, 1802) was recovered from 25 marine mammals representing 12 species in two orders from four geographical localities. Five new cyst morphotypes are described. Comparison of mean measurements of each morphotype with the others suggests that *P. delphini* may represent more than one species. New host records for *P. delphini* are reported for *Tursiops gilli* Dall, *Pontoporia blainvillei* Gervais, and *Lagenodelphis hosei* Fraser. An apical sucker is noted for the first time on *Monorygma grimaldii*.

Department of Biology, California State University, Long Beach, California 90840. Present address of Testa: Department of Biology, Wayne State University, Detroit, Michigan 48202.

Since its discovery in the early 1800's, large numbers of a larval cestode have been recovered from the blubber of numerous marine mammals throughout the world. First described by Bosc (1802) under the name of *Hydatid delphini*, this worm has since been the subject of many publications.

It has generally been accepted that there are at least two kinds of phyllobothriid cysts found in marine mammals, namely *Phyllobothrium delphini* (Bosc, 1802) from the blubber, and *Monorygma grimaldii* (Moniez, 1889) from the mesenteries of the body cavity. Baer (1932) recognized two groups of phyllobothriid larvae in marine mammals which he named "delphinii" and "grimaldii." Scolices of the "delphinii" group were at the ends of short (12–15 mm) invaginations while those of the "grimaldii" group were at the ends of long (12–100 cm) filament-like invaginations. Baylis (1932) listed five species of *Phyllobothrium* larvae with a total of ten synonyms, three species of *Monorygma* with seven synonyms, and *Scolex delphini* Stossich 1898 from cetaceans. Literature reviews have been published by Dollfus (1964a) and Guiart (1935).

In his discussion of *P. delphini*, Guiart (1935) described four cyst types, emphasizing that he was not trying to determine whether the larvae were different stages of the same species or different species of worms. Delyamure (1955) accepted Guiart's types and described two additional ones.

There still remains some confusion as to the relationship of *M. grimaldii* to *P. delphini*. Williams (1968) discussed the former under the name of *P. chamissonii* (Linton, 1905).

The present study was conducted to determine the systematic position of *M. grimaldii* in relation to *P. delphini* and to compare the morphology of the latter according to morphotype, different host individuals, and different host species from four geographical locations. The possibility of the existence of more than one cosmopolitan species was also examined.

Table 1. Zoogeography of *Phyllobothrium delphini* morphotypes. Parentheses indicate number of host individuals examined.

	Types											Total larvae examined per locality	
	1	2	3	4	5	6	7	8	9	10	11		
Southern California													
<i>Delphinus delphis</i> (8)			1	14			4		1		4		
<i>Lagenorhynchus obliquoides</i> (4)		1	1	10	2		1	1					
<i>Lissodelphis borealis</i> (4)				8			4			2			
<i>Phocoenoides dalli dalli</i> (1)				2									
<i>Tursiops gilli</i> (1)							1				1		
No. of each type examined		1	2	34	2		10	1	1	2	5	58	
Africa													
<i>Arctocephalus pusillus</i> (1)										2			
<i>Lagenodelphis hosei</i> (1)			1	1	4			1					
<i>Lagenorhynchus obscurus</i> (1)									2				
<i>Stenella graffmani</i> (1)		1			2								
No. of each type examined		1	1	1	6			1	2	2		14	
Florida													
<i>Kogia breviceps</i> (1)			2	1						1	1		
<i>Stenella caeruleoalba</i> (1)				2			1						
No. of each type examined			2	3			1			1	1	8	
Hawaii													
<i>Stenella longirostris</i> (1)								1					
No. of each type examined								1					
Total number examined		—	2	5	38	8	—	11	3	3	5	6	81

Materials and Methods

Phyllobothrium delphini cysts were obtained from 25 host individuals, representing 12 species of marine mammals in two orders from four geographical localities (Table 1). Host taxonomy follows that of Rice and Scheffer (1968).

With the exception of one sample collected by the junior author, all southern California samples were collected by Mr. William Walker while Curator at Marineland of the Pacific. Of these, three were from captured animals that died in captivity; the remainder from beach strandings. Cysts were received fixed *in situ* in 10% formalin or alive in the blubber. Live larvae were excised and fixed in AFA or Bouin's solution.

Hawaiian, Floridian and African samples were fixed *in situ* or free from the blubber in formalin. A single larva from *Pontoporia blainvillei* from South America was dehydrated upon arrival and unsuitable for further examination.

Cysts from *Kogia breviceps* and *Arctocephalus pusillus* were sectioned at 15 m μ , those from remaining hosts at 25 m μ . All were stained in Delafield's hematoxylin and counterstained in eosin.

Gross measurements of length and width of longitudinal sections of bladder were made with a centimeter ruler, all others by ocular micrometer. All measurements are in millimeters unless otherwise stated. Measurements considered

Table 2. Measurements of previously described morphotypes of *Phyllobothrium delphini*.

Character	Type			
	2	3	4	5
Bladder				
Long	2.8-3.5 (3.1)	5.4-9.0 (7.5)	3.5-9.5 (6.3)	4.0-6.5 (5.0)
Wide	1.5-1.7 (1.6)	4.0-4.5 (4.1)	2.0-6.5 (3.4)	2.5-6.0 (4.0)
Wall Thick	0.102-0.326 (0.214)	0.468-0.958 (0.705)	0.048-1.428 (0.827)	0.286-0.652 (0.471)
Neck				
Long	1.26-1.43 (1.35)	3.77-7.75 (6.09)	2.86-8.16 (4.72)	2.14-3.98 (2.93)
Wide	—	0.550-0.958 (0.802)	0.714-1.530 (1.077)	0.673-1.530 (1.151)
Ratio Bladder				
L to Neck L	1.9-2.7 (2.3)	—	1.01-1.80 (1.35)	1.26-2.12 (1.59)
Scolex				
Long	0.714-0.913 (0.814)	0.714-1.124 (0.898)	0.612-1.326 (1.032)	0.612-1.122 (0.887)
Wide	0.469-0.673 (0.571)	0.918-1.183 (1.122)	0.685-1.570 (1.172)	0.673-1.040 (0.856)
Acc. Sucker				
Diameter	0.113-0.162 (0.133)	0.162-0.218 (0.190)	0.145-0.284 (0.196)	0.145-0.218 (0.181)
Apical Sucker				
Long	0.046-0.065 (0.056)	0.051-0.085 (0.065)	0.036-0.091 (0.059)	0.055-0.081 (0.066)
Wide	0.046-0.065 (0.056)	0.040-0.091 (0.069)	0.042-0.111 (0.070)	0.051-0.087 (0.066)
Ex. Tubules				
Diameter	0.014-0.038	—	—	0.010-0.063
No. Examined	2	5	38	8

include length and width of bladder (as measured from the outer surface), thickness of bladder wall, length and width of neck and scolex, diameter of accessory suckers, length and width of apical sucker, and diameter of excretory tubules within the bladder wall.

Eighty-one larvae were sectioned and measured. Numbers of larvae examined from each host species and locality are listed in Table 1.

For comparison, several scolices of *Monorygma grimaldii* were embedded in paraffin, sectioned at 15 $m\mu$, stained in Delafield's hematoxylin and counterstained in eosin. Other scolices were teased out of the invaginated neck, stained in acetocarmine, and mounted in piccolyte.

Results

All scolices of larvae recovered from the blubber were typical for *P. delphini*, being composed of four ruffled bothridia each bearing an anterior accessory sucker. A fifth (apical) sucker was present on the myzorhynchus. During this study, four of the six existing cyst morphotypes were encountered (Figs. 1a-f). As previous descriptions are incomplete, their measurements (taken from this study) are given in Table 2. Five new types were also found (Figs. 1g-k). Their measurements are given in Table 3.

Remarks.—There were similarities observed between two of the existing morphotypes as listed by Guiart (1935) and Delyamure (1955) and four of those found during this study. Type 7 (Fig. 1g) is similar to their Type 4 (Fig. 1d), in that the in-

Table 3. Measurements of previously undescribed morphotypes of *Phyllolobothrium delphini*.

Character	Type					
	7	8	9	10	11	
Bladder						
Long	3.2-6.5 (5.0)	8.0	5.0-8.5 (6.7)	3.5-11.0 (6.7)	5.0-9.5 (6.5)	
Wide	3.0-5.5 (3.5)	3.5-4.5 (3.8)	5.0-6.0 (5.5)	2.5-4.5 (3.4)	3.0-4.0 (3.6)	
Wall Thick	0.408-0.877 (0.765)	0.469-0.673 (0.598)	0.612-0.918 (0.734)	0.408-0.551 (0.462)	0.571-0.979 (0.773)	
Neck						
Long	4.28-8.97 (5.62)	6.12-7.65 (6.66)	6.32-9.59 (8.36)	2.24-5.04 (3.59)	3.89-7.96 (4.23)	
Wide	0.714-1.224 (0.982)	0.612-0.918 (0.775)	0.816-1.305 (1.074)	0.979-1.632 (1.278)	1.122-1.693 (1.377)	
Ratio Bladder						
L to Neck L	0.68-0.98 (0.83)	1.05-1.31 (1.21)	0.71-0.89 (0.80)	1.56-2.25 (1.84)	1.20-1.63 (1.34)	
Scolex						
Long	0.612-1.224 (0.863)	0.816-1.326 (1.020)	1.122-1.428 (1.265)	0.673-1.428 (1.152)	0.775-1.428 (0.989)	
Wide	0.816-1.428 (1.124)	0.775-1.693 (1.244)	0.979-1.305 (1.189)	0.551-1.385 (0.944)	0.857-1.224 (1.047)	
Acc. Suckers						
Diameter	0.145-0.243 (0.186)	0.162-0.218 (0.198)	0.203-0.267 (0.239)	0.146-0.267 (0.198)	0.170-0.218 (0.192)	
Apical Sucker						
Long	0.040-0.065 (0.058)	0.063-0.067 (0.065)	0.057-0.085 (0.071)	0.050-0.107 (0.086)	0.048-0.077 (0.067)	
Wide	0.050-0.081 (0.066)	0.069	0.071-0.097 (0.084)	0.068-0.123 (0.104)	0.055-0.085 (0.067)	
Ex. Tubules						
Diameter	0.010-0.095	0.030-0.061	0.019-0.076	0.012-0.036	0.016-0.051	
No. Examined	11	3	3	5	6	

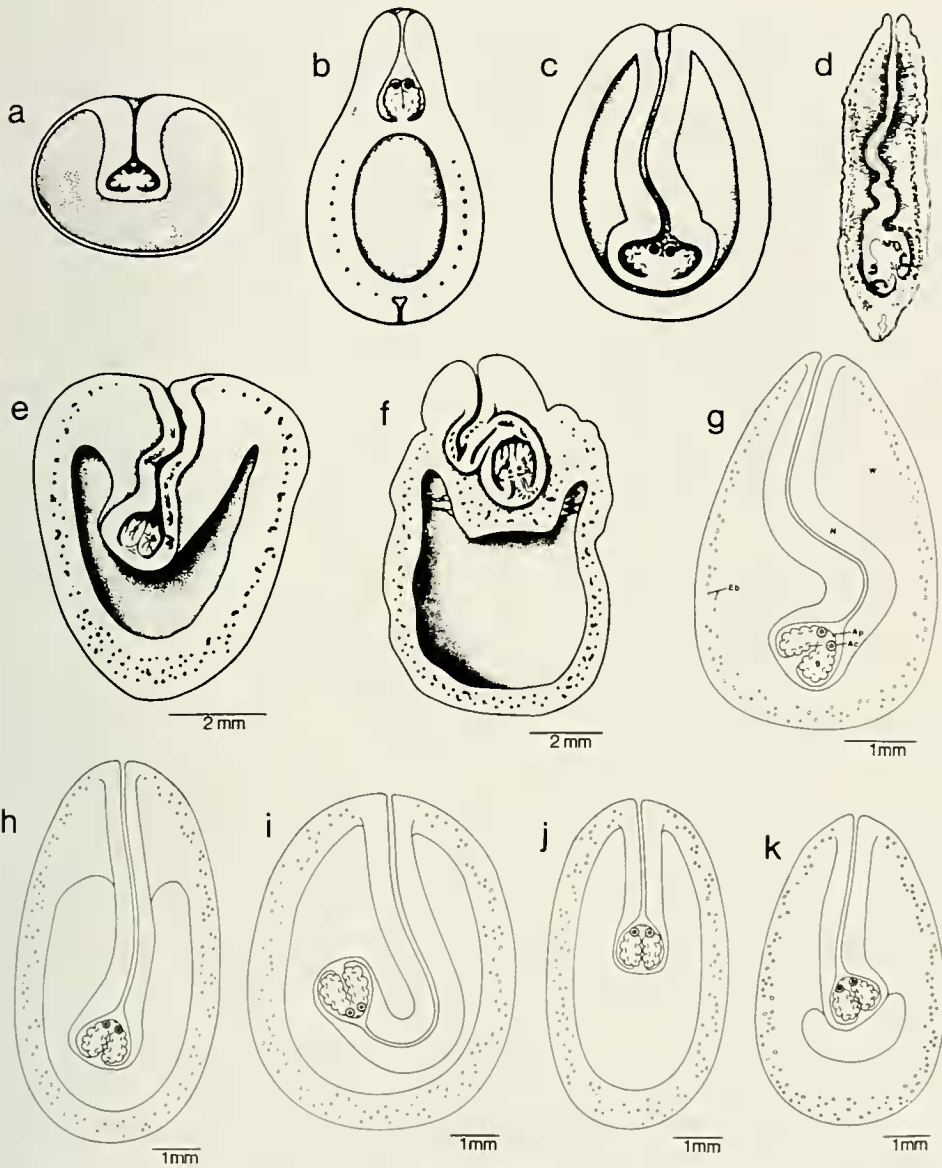


Fig. 1. Morphotypes of *Phyllobothrium delphini*: a-c, morphotypes 1-3 (Guiart, 1935); d, morphotype 4 (Baer, 1932); e-f, morphotypes 5-6 (Delyamure, 1955); g-k, morphotypes 7-11 (original). Ac, accessory sucker; Ap, apical sucker; B, bothridium; Eb, excretory tubules of bladder wall; N, invaginated neck; W, bladder wall. (No size scales available for Figs. 1a-d.)

vaginated neck and scolex are in contact with the bladder wall. However, it differs from Type 4 (as figured by Baer [1932] and described by Guiart [1935]) in ratio of bladder length to neck length (greater than one in Type 4). Type 8 (Fig. 1h) differs from the previously described Type 3 (Fig. 1c) in its thickness at the point of invagination. Types 9 and 10 (Figs. 1i and 1j), also similar to Type 3 (Fig. 1c), vary

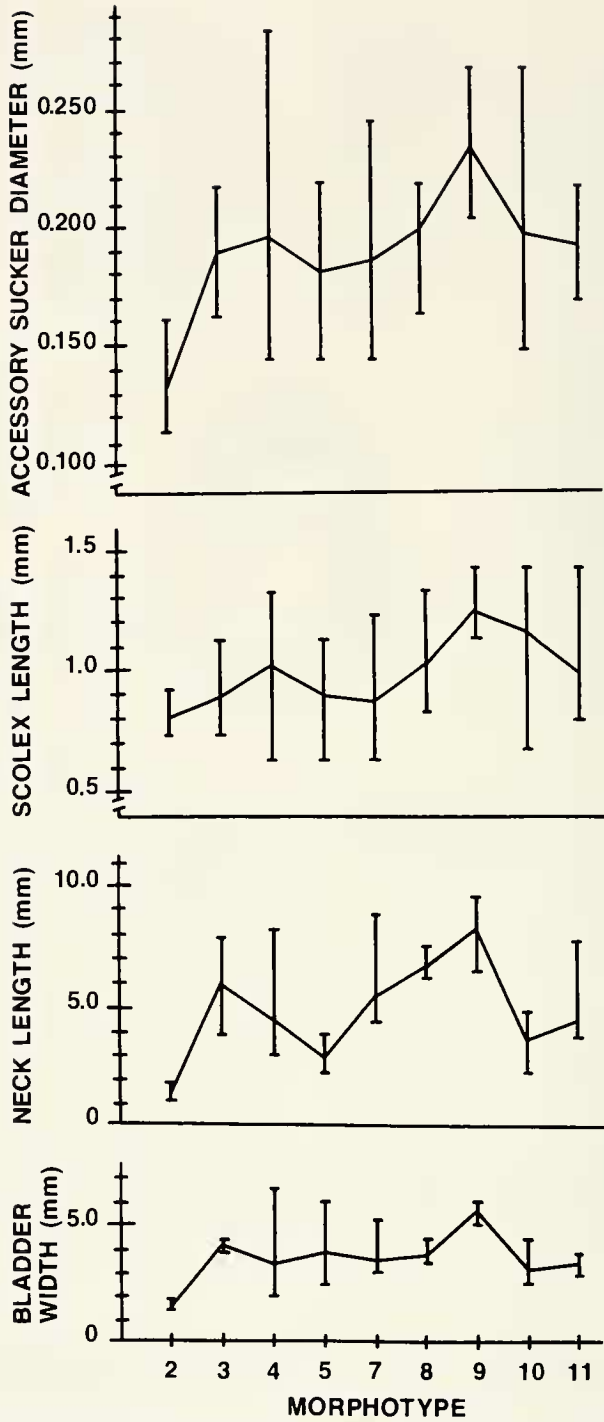


Fig. 2. Relationships of mean measurements for diameter of accessory sucker, length of scolex, length of neck, and width of bladder for each morphotype.

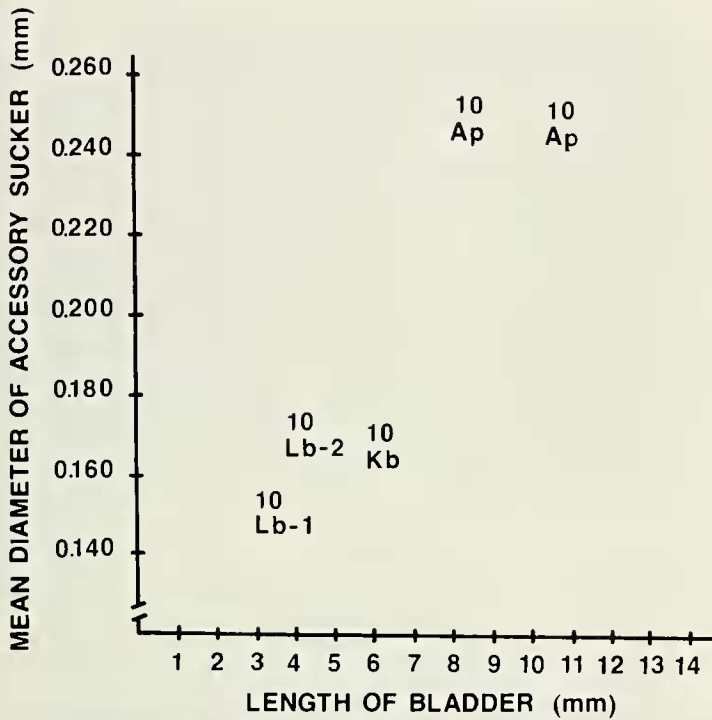


Fig. 3. Comparison of mean diameter of accessory sucker against length of bladder of morphotype 10 by host individual. Ap = *Arctocephalus pusillus*; Kb = *Kogia breviceps*; Lb 1 and 2 = *Lissodelphis borealis* 1 and 2.

in neck length-bladder length ratio (neck longer than bladder in Type 9 and reaching only to near center of bladder in Type 10).

No cysts of Types 1 or 6 were seen during this study. Delyamure (1955) described Type 6 as having accessory suckers at the "bottom" of the bothridia. The accessory suckers of all larvae examined were situated anteriorly.

New host records are noted for *Tursiops gilli* from southern California, *Pontoporia blainvillei* from South America, and *Lagenodelphis hosei* from Africa.

Scolices of *M. grimaldii* were typical for that genus. The bothridia were sessile and oval with smooth margins, and each bore an anterior accessory sucker. An apical sucker on the myzorhynchus is reported for the first time.

Discussion

A comparison of *P. delphini* and *M. grimaldii* scolices indicates that they both should maintain separate generic status. Scolices of all *P. delphini* from this study were composed of four folded bothridia, each with an anterior accessory sucker and a fifth (apical) sucker on the myzorhynchus. The four bothridia of *M. grimaldii* are oval and smooth, each bearing an anterior accessory sucker in addition to an apical sucker on a relatively large myzorhynchus. This is the first report of a fifth sucker. It is possible that this structure was overlooked by previous authors, as it had been in *P. delphini*.

Neither Guiart (1935) nor Delyamure (1955) attempted to separate the larvae of *P. delphini* taxonomically by morphotype. For the purposes of this study their

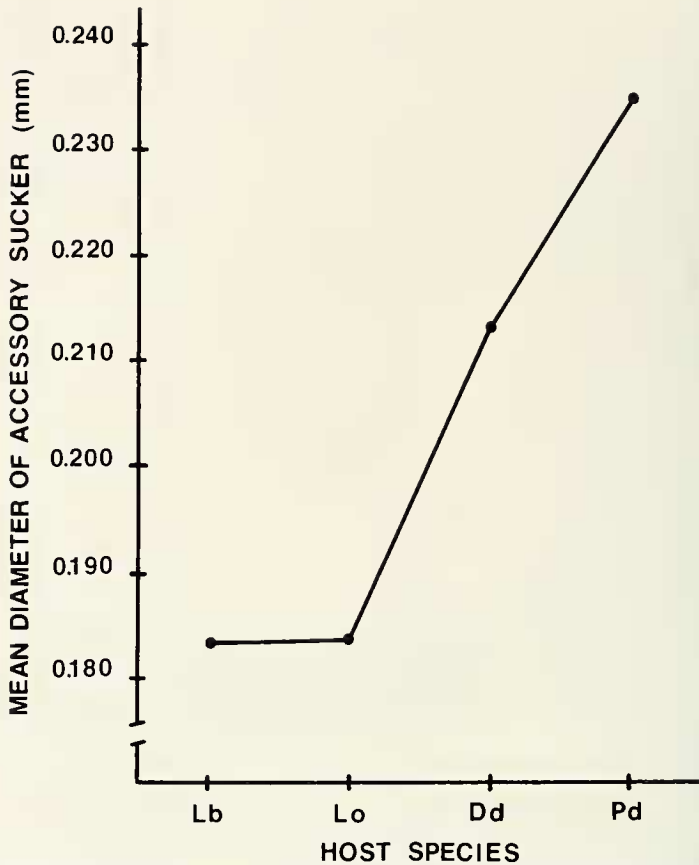
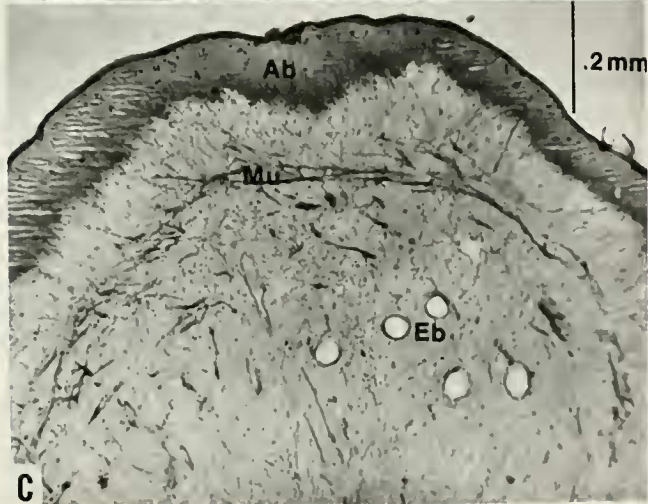
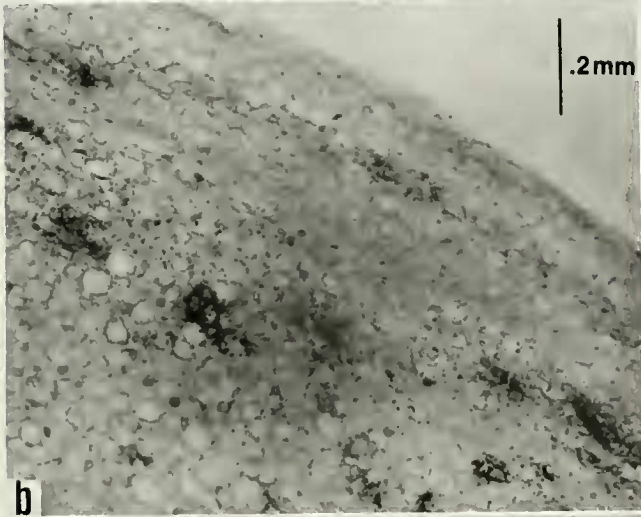
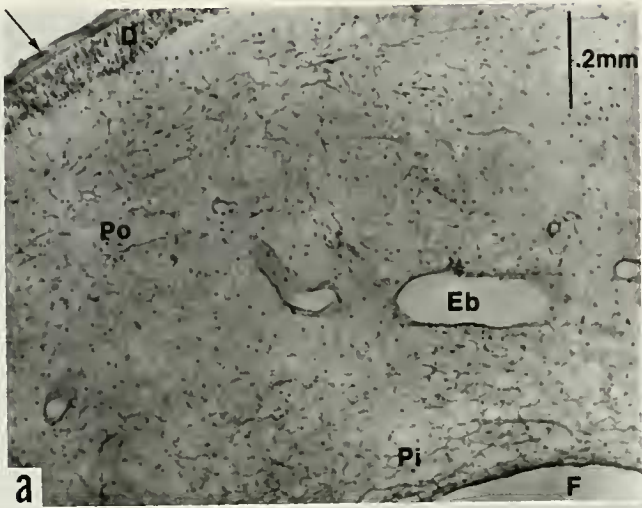


Fig. 4. Comparison of mean diameter of accessory suckers of morphotype 4 from different host species. Dd = *Delphinus delphis*; Lb = *Lissodelphis borealis*; Lo = *Lagenorhynchus obliquidens*; Pd = *Phocoenoides dalli dalli*.

types were accepted as valid morphological variants. New types encountered were grouped according to gross morphological appearance during the initial phase of our investigation. Mean body measurements of worms of a given morphotype, from a single host individual, or from a single host species were then compared with one another. Only when values for length of scolex and neck, width of bladder and diameter of accessory sucker were considered according to morphotype does a pattern emerge (Fig. 2). That is, for a given morphotype, body dimensions fell into a somewhat predictable range. This represents the possibility that each morphotype or group of related morphotypes may indeed represent separate species.

Fig. 5. Longitudinal sections of *Phyllobothrium delphini* bladder wall: a. Section through normal bladder wall; b. Section of abnormal bladder wall of a cyst recovered from *Delphinus delphis* (normal histology is absent from all parts of the bladder); c. Section through abnormal bladder wall of a cyst recovered from *Phocoenoides dalli dalli*. Ab = abnormal outer layer; D = dense layer of dark staining cells; Eb = excretory tubules of bladder wall; F = fluid filled portion of bladder; Mu = muscle fibers; Pi = inner layer of loose bladder parenchyma; Po = outer layer of parenchyma with muscle fibers; arrow indicates clear outer layer.



Numbers of individuals of each morphotype are listed in Table 1 according to locality and host species. It is apparent that members of a type class can be found in different localities, host species and even different orders. There is also a variation in the distribution of morphotypes. Type 4 was the most commonly encountered larva in southern California, while Type 5 was most frequent in Africa. This, in all probability, reflects the distribution of adult worms.

There is some indication of host influence on the larvae (Fig. 3). The number of cysts is too small to be able to draw any firm conclusions, but the suggestion is that at least different orders of marine mammals may play a role in determining the overall size of the cysts. Data shown in Fig. 4 supports this idea, showing differences in accessory sucker diameter for a large number of worms of the same morphotype taken from different host species. Further evidence comes from the fact that, regardless of morphotype, the bladder walls of all larvae recovered from a particular host individual were histologically alike, whether normal (Fig. 5a) or not (Figs. 5b and 5c). Abnormal appearances could not be attributed to post-mortum degradation.

Just how the marine mammal becomes infected with *P. delphini* is still a matter of conjecture. Skrjabin (1972) eliminated krill as the possible primary intermediate host, due to the fact that odontocete and baleen whales which had fed on fish were heavily infected, while those baleen whales which had fed on krill were rarely infected. He found that *Phyllobothrium* larvae from squids were digested in the whale's stomach while *Scolex pleuronectis* larvae entered the mucous membranes of the gut. From this Skrjabin (1972) concluded that *S. pleuronectis*, taken with a fish meal, burrowed through the gut wall and entered the circulatory or lymphatic system. From there they settled in the blubber and through a series of transformations came to look like *P. delphini*. He and Euzet (1959) reported having seen all phases of this transformation, but Dollfus (1964b) did not.

Partial argument against this idea is given by Skrjabin (1972) in his statement that dolphins of the Black Sea are not parasitized by *P. delphini* even though the local fish are infected with *S. pleuronectis*.

The recent work of Hamilton and Byram (1974) provides additional insight into this problem. They induced in vitro transformation of a plerocercoid with quadriloculate bothridia taken from the gastropod *Fasciolaria tulipa* to a larva with triloculate bothridia, one pair of bifurcated hooks, an accessory sucker and muscular pad. These changes placed the worm in the genus *Acanthobothrium* van Beneden, 1849. Their (Hamilton and Byram, 1974) figure of the untreated larval scolex is like that of *Scolex polymorphus trilocularis* illustrated by Dollfus (1964b, fig. 16). This raises the possibility that the *Scolex* larvae are onchobothriids as adults, introducing once again the problem of an elasmobranch cestode infecting marine mammals.

If Skrjabin's (1972) observation that *Phyllobothrium* larvae in squid are digested in the whale's stomach is typical, one would expect the same fate for those larvae in teleosts. There must then be another mode of infection, possibly through the proceroid taken with a fish or squid that had recently fed on an infected crustacean. If "activation" (i.e. stimulation of the larva to begin the next stage of development) of the proceroid in the fish or squid has taken place, the stimulus may be sufficient to allow development of the larva into a plerocercoid in the marine mammal. This idea is consistent with Skrjabin's (1972) statement that the



Fig. 6. *Phyllobothrium delphini* in blubber of *Delphinus delphis*.

krill-eating baleen whales, which accidentally ingest an occasional fish, are only rarely infected with *P. delphini*.

It appears possible that sharks become infected with *P. delphini* by eating the flesh of marine mammals, since these larvae are such common parasites of the blubber (Fig. 6). Southwell and Walker (1936) note that "cysticerci found in seals are capable of retaining their viability for at least 11 days after death of the host." During the present study, larvae in the blubber were viable after being stored at 4°C for one month.

Shark attacks on cetaceans have been previously reported (Wood et al., 1970). Ridgway and Dailey (1972) show evidence of an attack on a common dolphin (*Delphinus delphis*) by a mako shark (*Isurus oxyrinchus*, according to tooth pattern) that occurred along the southern California coast. The Greenland shark, *Somniosus microcephalus*, is known to bite off the flesh of living whales (Johnston, 1937, according to Williams, 1968).

Additional work is underway using experimental infections and *in vitro* cultivation to answer the remaining questions on the transmission, distribution and speciation of *P. delphini*.

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Literature Cited

- Baer, J. G. 1932. Contribution à l'étude des Cestodes Cétacés. *Rev. Suisse Zool.*, 39:195-228.
- Baylis, H. A. 1932. A list of worms parasitic in Cetacea. "Discovery" Rep., 6:395-418.
- Bosc, L. A. G. 1802. Histoire naturelle des Vers, contenant leur Description et leurs Moeurs. (*In* Buffon, Histoire Naturelle, ed. R. R. Castel (Suite).) 3 Tom., Paris (from Dollfus, 1964a).
- Delyamure, S. L. 1955. Gel'minto fauna morskikh mlekapitayushchikh v suete ikh ekologii i filogenii. Izd. Akad. Nauk. SSSR, Moscow. 517 pp. (English translation by M. Raveh, 1968. Helminthofauna of marine mammals (ecology and phylogeny). Israel Program for Scientific Translation, Jerusalem, 552 pp.).
- Dollfus, R. Ph. 1964a. A propos de la récolte, a Banyuls d'un cystique de cestode chez *Tursiops truncatus* (Montagu, 1821). Les cystiques de cestodes chez les cétacés et pinnipeds. *Vie Milieu.*, 17:177-204.
- . 1964b. Énumération des cestodes du plancton et des invertébrés marins (6^e contribution). *Ann. Parasit. Hum. Comp.*, 34:329-379.
- Euzet, L. 1959. Recherches sur les Cestodes Tétraphyllides des Sélaciens des Côtes de France. Thèse Fac. Sci. Univ. Montpellier, 263 pp.
- Gniart, J. 1935. Cestodes parasites provenant des campagnes scientifiques de S.A.S. le Prince Albert 1^{er} (1886-1913). *Résult. Camp. Scient. Prince Albert*, 1(91):1-100.
- Hamilton, K. A., and J. E. Byram. 1974. Tapeworm development: The effects of urea on the larval Tetracyllidean. *J. Parasitol.*, 60:20-28.
- Johnston, T. H. 1937. The Cestoda of the Australasian Antarctic Expedition. *Scient. Rep. Australas. Antarct. Exped.*, 10:1-74 (from Williams, 1968).
- Rice, D. W., and V. B. Scheffer. 1968. A list of marine mammals of the world. U.S. Fish and Wildlife Serv. Special Sci. Report. Fisheries No. 579, p. 12.
- Ridgway, S. H., and M. D. Dailey. 1972. Cerebral and cerebellar involvement of trematode parasites in dolphins and their possible role in strandings. *Wildlife Diseases*, 8:33-43.
- Skrjabin, A. S. 1972. (Larvae of cestodes of the genus *Phyllobothrium* Van Beneden, 1850 (Tetracyllideae), parasites of whales and other marine animals.) *Parasitology*, 6(5):426-434. (In Russian; English summary, p. 434.) English translation by Elzbieta Szuladzinski, Department of German, Classic and Eastern Languages, California State University, Long Beach.
- Southwell, T., and A. J. Walker. 1936. Notes on a larval cestode from a fur seal. *Ann. Trop. Med. Parasitol.*, 30:91-100.
- Williams, H. H. 1968. The taxonomy, ecology and host specificity of some Phyllobothriidae (Cestoda: Tetracyllideae). *Philos. Trans. Roy. Soc. London, Ser. B, Biol. Sci.*, 253:231-307.
- Wood, F. G. Jr., D. K. Caldwell, and Melba C. Caldwell. 1970. Behavioral interactions between Porpoises and Sharks. *In* Investigations on Cetacea, G. Pilleri, ed., 2:264-277.

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